The University of Chicago

INHERITANCE OF ALEURONE COLOR IN MAIZE

A DISSERTATION

SUBMITTED TO THE FACULTY
OF THE OGDEN GRADUATE SCHOOL OF SCIENCE
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

BY

MERLE CROWE COULTER

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INHERITANCE OF ALEURONE COLOR IN MAIZE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 265

MERLE C. COULTER

Interested in the pedagogical value of plant genetics, the writer was impressed with the fact that the bulk of our knowledge comes from experiments with corn. An investigation was undertaken, therefore, with no more definite object than to discover how dependable some of these classic experiments actually are. During three years of rather interrupted and limited investigation, this undertaking, as might be expected, has been rewarded by numerous results that have been interesting and suggestive, but by practically none that as yet can be regarded as conclusive. In view, however, of the number of investigators, professional and amateur, who are now interested in inheritance in corn, it is felt that a brief statement of a few of the results may be useful.

Technique

The writer's experiences in matters of manual technique will undoubtedly be of interest to amateurs. The grosser mechanics of corn crossing are simple and familiar. The difficulties are mainly two: (1) to avoid exposing the silks to chance foreign pollen at the time the cross is made, and (2) to insure full pollination, and hence full ears. It is common practice to remove, totally or partially, the bag which covers the silks when the pollen is applied. This involves momentary exposure of the silks to chance foreign pollen, plenty of which is almost sure to be circulating in the air. Thorough distribution of the applied pollen over the silks is then attempted by shaking the bag in some way. In the hands of an experienced operator this method is not only adequate but rapid. When the writer attempted this, however, the results were not satisfactory. Less than half the ears were fully pollinated, and there were quite a number of cases in which about 5 or 6 grains of foreign pollen had evidently been admitted. For the second season's work, therefore, a simple mechanical device was employed,

and this effectually solved the difficulties. This is a so-called corn-pollinator, a description of which has already been published.[1] Even in inexperienced hands this method will not only insure full pollination, but will never admit foreign pollen. Its drawback lies in the fact that it lengthens the process somewhat; hence it is felt that this device may be recommended to all save experienced operators, who are conducting extensive experiments.

Normal ratios

An attempt was made to discover how exactly certain complex ratios might be predicted. Material was sought in which a number of factors could interact to produce various but predictable (?) ratios. Nothing was more suitable than the set of factors involved in the inheritance of aleurone color in corn. These factors have already assumed an important rôle in pedagogy. R and C are complementary factors, the presence of both being required for the production of red aleurone, and P^2 is a supplementary factor which changes red to purple (PRC is purple, pRC red, PrC white). Other factors have been added to this set by EAST and EMERSON, but they are not dealt with in this paper. The original stock material was furnished by EAST, to whom the writer wishes to express his appreciation.

Leaving out of consideration those well established cases in which a 1:0 or 3:1 ratio is produced, it was found that the material, as originally provided, could be manipulated to produce 8 different ratios. Appropriate crosses were made, therefore, and of the resulting crop all ears containing 64 or more grains are considered in the following summary.

I.—0:1:1 (no purple:50 per cent red:50 per cent colorless) ratio predicted; from pprrCC×ppRrCC and reciprocal. Eight ears gave a total of 0 purple:559 red:659 white, or an average

[1] BOT. GAZ. 58:63. 1919.

[2] EAST and HAYES use the symbol P for this factor, while EMERSON uses Pr for what is probably the same factor.

EAST, E. M., and HAYES, H. K., Inheritance in maize. Conn. Agric. Exp. Sta. Bull. no. 167. pp. 142. *pls. 25.* 1911.

EMERSON, R. A., A fifth pair of factors, Aa, for aleurone color in maize, and its erlation to the Cc and Rr pairs. Cornell Univ. Agric. Exp. Sta. Mem. 16 pp. 231–289. 1918.

ratio of 0:0.92:1.08. The extreme ratios on individual ears were 0:0.81:1.19 and 0:1.03:0.97. Conclusion: slight but chronic excess of colorless grains.

II.—0:9:7 predicted; from ppRrCc selfed. Five ears gave 0:418:320, or an average ratio of 0:9.06:6.94. Extreme ratios on individual ears, 0:8.77:7.23 and 0:9.45:6.55. Conclusion: predictions fulfilled.

III.—0:3:5 predicted; from ppRrCc×pprrCc. Three ears gave 0:260:430, or an average ratio of 0:3.01:4.99. Extreme ratios on individual ears, 0:3.19:4.81 and 0:2.94:5.06. Conclusion: predictions fulfilled.

IV.—1:1:2 predicted; from pprrCC×PpRrCc. Only one ear with over 64 grains obtained.

V.—9:9:14 predicted; from ppRrCc×PpRrCc. Four ears gave 229:242:262, or an average ratio of 10.11:10.35:11.54. Extreme ratios on individual ears, 10.14:12.69:9.17 and 6.51:9.83:15.55. Conclusion: decided but not chronic excess of colored grains.

VI.—3:3:10 predicted; from ppRrCc×PprrCc and pprrCc× PpRrCc. Eight ears gave 252:235:765, or an average ratio of 3.22:3.00:9.78. Extreme ratios on individual ears, 3.60:2.07: 10.33 and 4.42:3.58:8.00. Conclusions: predictions fairly well fulfilled, considering smallness of population used.

VII.—9:3:20 predicted; from PprrCc×PpRrCc. Only one ear obtained with over 64 grains.

VIII.—27:9:28 predicted; from PpRrCc selfed. Thirteen ears gave 1534:464:1560, or an average ratio of 27.59:8.35:28.07. Extreme ratios from individual ears, 23.54:9.92:30.54 and 28.97:11.03:24.00. Conclusions: predictions well fulfilled; slight tendency toward excess of purple at expense of red (as was regularly the case except, strangely enough, in the two individual ears cited under extreme ratios) may well be accounted for by improper classification, throwing a few deep red grains with the purple.

From this preliminary experiment the general conclusion was drawn that ratios produced by the interaction of these three factors were sufficiently distinct to be readily recognized in the vast majority of cases. This was confirmed by later experience,

which included also several other types of ratios produced by these same factors. Actually the only difficult distinction which was encountered was between 9:9:14 and 3:3:2, for the former (V) commonly showed a deficiency of colorless grains. How persistent and significant this deficiency is I will not venture to conclude from the limited data. Elsewhere recognition was easy so long as P, R, and C were the only factors dealt with.

Dominance

The literature is likely to leave one with the impression that dominance is complete with this set of factors. Uncertain on this matter, the writer wondered whether there was any hope of distinguishing genotypes from superficial appearance. In other words, was a grain with the formula ppRRCC a very dark red, ppRrCC or ppRRCc a lighter red, and ppRrCc a still ligher red? That such a thing might be possible was suggested by the following observation. When individuals of the formula ppRRCC were selfed, they regularly produced ears on which all of the grains were not only red but the same intensity of red. Obviously the grains were all of the same (ppRRCC) genotype. Likewise, ppRrcc× pprrCC would produce ears on which only 50 per cent of the grains were red, but always the same intensity of red. Here, also, all the red grains would be of the same (ppRrCc) genotype. In contrast with this were ears so produced that the colored grains represented more than one genotype. It was common in such cases for quite a series of color intensities to appear. Whether these different intensities to any degree represented the different genotypes was an open question, but one that could be readily decided.

An ear was chosen which had been produced by ppRrCc× PpRrCc. This particular ear was noteworthy in two respects. In the first place, where it should have shown a 9:9:14 ratio it actually gave 57:61:57. In the second place, an unusual range of color intensities appeared. Now the 9 purples theoretically should have been distributed among the following genotypes: 1 PpRRCC : 2 PpRrCC : 2 PpRRCc : 4 PpRrCc; the 9 reds, 1 ppRRCC : 2 ppRrCC : 2 ppRRCc : 4 ppRrCc. The writer therefore classified the grains on the basis of color intensity, with some

hope that four intensities of each color could be recognized. This proved impossible, since the series of intensities was practically continuous. At this point, therefore, I was forced to conclude that at least genotypes could not be sharply separated on the basis of color intensity. There yet remained the possibility, however, that color intensity might to some degree depend on genotype, the boundaries of the classes merely being obscured by individual variation. With this in view the whole series of colored grains was arbitrarily divided into several intensity classes, and these classes were planted separately and selfed.

Class W, indicating colorless, gave six large ears, all of which, of course, showed 100 per cent colorless grains.

Class R indicated faint red. This was the minimum color intensity, and may best be described by saying that a casual glance would discover no color in such grains. More careful scrutiny, however, reveals an evenly distributed (not mottled or variegated) but very faint aleurone color. In the original count of the parent ear these grains had been classified as red. Only one ear was obtained from this class, but that was very striking. Most of its grains were colorless, but some were the same faint red as the parent, and absolutely none were of any deeper intensity. Viewed at a little distance, this ear would be said to contain 100 per cent white grains.

Class R′, indicating light red, produced two ears, on which the ratios were 0:42:31 and 0:88:54 respectively. Without hesitation these were both diagnosed as 0:9:7 ratios, indicating a ppRrCc genotype.

Class R″, indicating red, produced three ears, with respective ratios of 0:76:59, 0:176:63, and 0:24:8. One feels safe in calling the first a 0:9:7 and the last two 0:3:1 ratios. The conclusion from this is that ppRrCC or ppRRCc or both have a tendency to produce a more intense aleurone color than does ppRrCc. The question arises whether the appearance of one 0:9:7 ratio from the red class was due to improper delimitation of the classes in the first place, of which there was, of course, every possibility; or whether it might have been due to inevitable overlapping of the classes owing to individual variation. I am in no position to

answer this, since I cannot say whether the particular grain which gave the 0:9:7, although included in the red class, was noticeably lighter than the other two.

Class R‴ indicated dark red (or purple?). In the original count these grains had been included with the red, but the intensity of color was such that it demanded close scrutiny to distinguish them from the purple. Four ears came from this class. Of these, one gave 0:130:33, and the other three 0:200:0 (no exact count was made of large homogeneous ears). The first was evidently a 0:3:1, with an excess of red grains, while the others obviously represented the ppRRCC genotype, the conclusions suggested being similar to that of class R″.

Class P indicated faint purple, with the same significance as R for faint red. This class gave three ears, as follows:

Faint purple	Faint red	Colorless
5	4	21
53	36	141
51	14	141

No attempt is made at present to attach any significance to these counts. In fact, it is felt that such counts are rather untrustworthy, since the color is frequently so faint as to lie at the very limit of visibility. Sufficient at present that not so much as a single light purple or light red was produced on these ears; only the faint color of the parents was regularly produced.

Class P′ indicated light purple, and gave three ears, 142:47:52, 34:14:40, and 13:1:12. The first is probably a 9:3:4 and the others 27:9:28 ratios.

Class P″ indicated dark purple, and gave one ear, 79:34:85, probably a 27:9:28 ratio with an excess of red.

The general conclusion from the preceding is that genotypes may be distinguished, to a degree, on the basis of color intensity, at least among red grains. One rather familiar with the material should be able to pick out a given genotype in most cases, particularly if he discarded intermediates, which the writer did not.

Returning now to the faint grains, one is confronted by three possible explanations: (1) these are grains, properly colored, in which an inhibitor tends to lessen materially the intensity of the

color; (2) they are grains, properly colorless, in which there is some partial substitute for the R or C (probably the latter, referred to later) factors or both; (3) they represent something entirely unrelated to the set of factors under discussion. That the second is a likely explanation is suggested by three facts.

1. The count of the original parent ear showed a marked deficiency of colorless grains. The faint red and faint purple grains had, in that count, been classified as colored. If they were truly colorless grains the original ear would have very closely approximated the predicted 9:9:14 ratio.

2. The nature of the original cross was such that every grain must be Pp or pp, but never PP. Inbreeding, therefore, might give ears with some red and no purple grains, but could never give ears with some purple and no red grains. Actually that is what occurred. This is, of course, merely negative evidence. Positive confirmation, however, comes from a similar experiment conducted with slightly different material. An ear produced by PpRrCc selfed, which gave an ideal 27:9:28 ratio, was used as the basis of an experiment similar to the preceding. The general results were about the same and need not be discussed in full. Among the purple grains, however, several produced ears which showed purple and colorless, but no red grains, and one produced a full ear of purple grains alone. This is to be expected from the fact that genotypes including PP, although not present in the previous ear, are present here. Such being the case, the behavior of the faint purple grains from this ear should prove significant. From that class came the following four ears:

Light purple	Faint purple	Faint red	Colorless
0	Some	Some	Many
0	Some	Some	Many
0	Some	0	Many
1	34	0	4

These certainly suggest the presence of PP in the last two cases, while Pp may be inferred for all the others. It is very likely that the last ear represents the homozygous condition for faint purple, whatever that may be, the color being present but indistinguishable in 4 grains.

3. EAST and HAYES (*loc. cit.*) describe in certain of their families grains which they call particolored. Their description leaves little doubt that the writer is dealing with the same phenomenon. These authors carried their work far enough to assign the P(R)c formula to these grains.

The tentative conclusion, therefore, may be reached that particolored (faint) grains lack C but contain some partial substitute. Just how this substitute is inherited is not clear as yet, but the fact that it is heritable is undoubted. It is probable, although not certain, that the same relationship between P and R as occurs in the inheritance of the normal full color maintains itself also under the particolored system. It must also be noted that this unknown substitute for C is by no means always effective in bringing any distinguishable color; its powers of expression seem to be limited by conditions, a matter which will be discussed later.

The question is now raised whether, in view of the possibility of a complete series of color gradations, reliable counts of purple, red, and colorless phenotypes can always be made. In answer one may safely state that the phenotypes stand out sharply unless particolored grains appear; the gap between light red and colorless is a wide one. Particolored grains by no means appear in all cases; the condition which brings them may or may not be present in the germ plasm. When they do appear, they do so in considerable numbers, so that a glance at the ear as a whole will determine whether or not one has them to deal with. Thereby the investigator is warned to focus sharply upon the boundary between light colored and particolored, but even under the most practiced eye some slight error is likely to creep in at this point.

An anomalous case

The possibility of at least partial substitution for the C factor has been mentioned. We may be dealing with something of the same sort in the following unusual case. EAST provided the writer with an ear produced by PPRrcc×pprrCC. The expectations were obviously fulfilled, half of the grains being purple and the other half colorless. The former, in the many crosses made, regularly revealed the PpRrCc formula, which was expected; while

the latter, in all cases but one, revealed PprrCc. In this one case the individual produced by this supposed PprrCc grain was selfed, and gave a ratio of 46:0:36. This is a perfect 9:0:7 ratio, such as would be produced by PPRrCc, but such a formula is out of the question in view of the history behind the ear. The obvious but heterodox suggestion is that some unusual condition is present, which, together with both P and C, results in purple aleurone; while with C alone it gives, not red, but colorless.

That this is a pathological case is suggested by two facts: (1) practically all the grains on this ear had their pericarps split irregularly, an unusual condition; (2) when planted, they germinated very slowly (or not at all), giving 3-inch plants at the time that all the neighboring rows had attained 3 or 4 feet; by harvest time a few small tassels had just appeared, but no silks.

Mottling

EMERSON (*loc. cit.*) has described the following situation in certain of his families. When the R factor enters the cross with the male parent only, a mottled aleurone results, while in all other cases a solid aleurone color is produced. Thus, RRcc×rrCC gives 100 per cent solid red; rrCC×RRcc gives 100 per cent mottled red; RRCC×RRcc gives 100 per cent solid red; RrCC selfed gives 50 per cent solid red, 25 per cent mottled red, and 25 per cent colorless.

The writer wishes to express his appreciation to EMERSON for providing material of the well known C tester and R tester. These races behaved with considerable regularity, for crosses between them consistently yielded 100 per cent solid purple grains when R tester was used as the male parent (PPRRcc×PPrrCC), and 100 per cent mottled grains when C tester was used as the male parent (PPrrCC×PPRRcc).

Splashed purple grains, recognized by EAST (*loc. cit.*) in most, but not all, of his families, were doubtless due to the same phenomenon. In the particular material of EAST's which was furnished, however, nothing of the sort could be identified, even in the very numerous cases in which the R factor came in with the male parent only. It was felt, therefore, that crosses between the material from EMERSON

and that from EAST would prove interesting. Evidently the former contains something which the latter lacks, and this something brings mottling instead of solid color, provided always the R factor comes in with the male parent only. Such crosses should help interpret this mottling, and should also reveal whether the P, R, and C factors of these two investigators are identical. Four crosses between C tester and EAST's material will be considered, with the families resulting therefrom.

TABLE I

EAR	CROSS	COLOR RATIO			MOTTLING RATIO		
		Predicted		Observed	Predicted		Observed
646	*PpRrCc* selfed.....	27:9:28	66:22:69	62:14:81	2:1	51:25	58:18
645	*PpRrCc* selfed.....	27:9:28	135:45:139	136:51:132	2:1	122:61	144:39
631	*PpRrCc* selfed.....	27:9:28	141:47:147	157:36:142	2:1	129:64	122:71
630	*PpRrCc* selfed.....	27:9:28	177:60:184	181:55:185	2:1	157:79	159:77
642	*PpRrcc* selfed.....	0:0:1	0:0:268	0:0:268	.....	.....	.....
643	*PpRrcc* selfed.....	0:0:1	0:0:461	0:0:461	.....	.....	.....
647	*PpRrCc*×pprrCc...	3:3:10	19:19:6	21:12:61	1:0	33:0	33:0
635	*PpRrCc*×pprrCc...	3:3:10	28:32:106	31:31:104	1:0	60:0	60:0
636	*PpRrCc*×pprrCc...	3:3:10	47:49:180	52:52:172	1:0	96:0	96:0
644	*PpRrcc*×pprrCc ...	1:1:6	8:8:49	9:9:47	1:0	18:0	18:0
652	*PpRrcc*×pprrCc ...	1:1:6	19:19:115	20:21:112	1:0	42:0	42:0
638	*PpRrCc*×PPRrCc..	9:0:7	88:0:68	74:0:72	2:1	49:25	52:22
649	PPRrCc×*PpRrCc*..	9:0:7	261:0:203	246:0:216	2:1	164:82	163:85
641	PPRrCc×*PpRrCc*..	9:0:7	159:0:123	156:0:126	2:1	104:52	106:50
640	PPRrCc×*PpRrCc*..	9:0:7	179:0:139	179:0:139	2:1	119:60	106:73
639	PPRrCc×*PpRrCc*..	9:0:7	314:0:234	313:0:235	2:1	209:104	259:54
650	PPRrCc×*PpRrCc*..	9:0:7	117:0:91	128:0:80	2:1	85:43	84:44
651	PPRrCc×*PpRrCc*..	9:0:7	224:0:174	239:0:159	2:1	159:80	161:78
648	PPRrCc×*PpRrcc* ..	3:0:5	63:0:104	63:0:104	2:1	42:21	44:19

I.—pprrCc (EAST)'×PPRRcc (C tester) gave 131:0:114 with all the purple grains mottled, according to expectations. Obviously these mottled purple grains represented a PpRrCc formula, the colorless PpRrCc. The number of this ear was 315, and its further behavior is recorded in table I, in which the italicized parent represents the immediate progeny of 315. Where mottling ratios are recorded, the solid color member always precedes (2:1 means 2 solid color : 1 mottled). Table I shows that predictions on the color ratios are fulfilled in all cases, with the possible exception of ear 638; while mottling ratios are similarly according to prediction with the possible (one feels like saying probable) excep-

tion of ear 639. It is a very striking fact that where no mottling is predicted (647, 635, 636, 644, 652) absolutely none appears.

II.—PPRRcc (C tester) ×ppRrCc (EAST) gave 62:0:52 with no mottling. Half the purple grains should have had the PpRRCc formula, the other half PpRrCc; the white grains, half PpRRcc, half PpRrcc. From the latter, two ears were selfed, both giving 0:0:300.

A cross was made between an individual resulting from one of the colorless grains as female parent, and ppRrCc as male parent. Since the former could be either PpRRcc or PpRrcc, we must consider both possibilities: (1) PpRRcc×ppRrCc would give 1:1:2 and no mottling (1:0); (2) PpRrcc×ppRrCc would give 3:3:10 and a mottling ratio of 2:1. The actual ratios were 48:28:78 and 76:0, satisfying 1.

Two crosses were made between individuals resulting from two of the colorless grains as male parents, and PPRrCc as female parent. The two possibilities are: (1) PPRrCc×PpRRcc would give 1:0:1 and 1:1; (2) PPRrCc×PpRrcc would give 3:0:5 and 2:1. One of the resulting ears actually gave 115:0:134 and 78:37. The color ratio might be either 1:0:1 or 3:0:5, but the mottling ratio decides the case in favor of 1. The other ear gave 242:0:278 and 126:116. There might be a slight doubt about the color ratio, but the mottling ratio decides in favor of 2.

Two other crosses in which 2:1 mottling ratios were predicted gave 73:38 and 162:65 respectively. We may conclude that this family also fulfils the predictions fairly well. It is interesting that cases in which the color ratio may be a matter of some doubt may sometimes be decided by reference to the mottling ratio.

III.—This family resulted from a cross reciprocal to the last, or ppRrCc (EAST) ×PPRRcc (C tester). This gave an ear containing only 13 grains, so that the ratios are without significance. The same possible genotypes are confronted as under II. One of the colorless grains inbred gave, of course, 0:0:300. A single individual, produced from one of the purple grains, was used as male parent three times, once on its own silks and twice on PPRrCc. If this individual had been PpRRCc, selfing should have given 9:3:4 and no mottling, while the cross indicated should have

given 3:0:1 and 1:1. If it had been PpRrCc, selfing should have given 27:9:28 and 2:1, the cross 9:0:7 and 2:1. Actually selfing gave 207:63:90 and 270:0, clearly indicating the former. In the two cases of the cross indicated, the actual color ratios were 411:0:127 and 360:0:129. These are 3:0:1 ratios, and satisfy, as before, the formula of PpRRCc for the male parent. The mottling ratios in these cases, however, were respectively 278:133 and 235:125. Obviously, where it was felt that 1:1 mottling ratios could be predicted with some certainty, the actual ratios obtained were strikingly close to 2:1. The writer fully realizes the care which must be exercised in classifying mottled grains. These particular ears were not only shelled (as usual), but were counted twice, using the same standards as proved satisfactory elsewhere. One is forced to conclude that these additional data represent an exceptional behavior, sufficiently decisive to be of some real significance.

IV.—pprrCC (EAST) ×PPRRcc (C tester) gave unusual data. It is unnecessary to give all of them; sufficient at present are the mottling ratios obtained. Four ears resulted in which mottling was to be expected in a 2:1 ratio. The actual ratios obtained were 155:0, 30:8, 151:3, and 177:3. Obviously the usual mottling situation is absent. The question arises whether the few so-called mottled grains were truly such. It is probable that they were not, since there have been known to occur various types of anomalous grains which may readily be confused with true mottling. Had these grains occurred on ears known to contain true mottling, they would have been included in that class. I feel justified, therefore, in the tentative conclusions that (1) the P, R, and C factors of EAST and EMERSON are probably identical; (2) mottling is due to a heritable factor (or factors) which is present in EMERSON'S C tester and absent in the material of EAST, and that this factor probably behaves immediately as a dominant, no matter with which parent it enters the cross. No attempt is made at present to explain the 2:1 mottling ratios which appeared in two cases of family III instead of the expected 1:1. As for family IV, this situation may be explained by assuming that not all of the C tester material was homozygous for the presence of the mottling factor.

The R tester material was similarly crossed with EAST's material. The color ratios obtained in five small families fully satisfied the predictions. The mottling ratios obtained, however, were quite different from those before, and may be summarized as follows: (1) ten ears gave 100 per cent colorless aleurone, and, of course, no mottling; (2) there were nine ears in which the R factor, wherever present, had come in with the female parent; in these, therefore, no mottling was to be expected; these gave a total of 889 self-colored grains to 1 mottled; (3) cases in which a 2:1 mottling ratio might have been expected may be taken up separately for the different families. Family I, produced by PpRrCc (EAST) ×PPrrCC (C tester), gave three such ears, with a total of 467 self-colored: 5 mottled grains (1.06 per cent mottling; extremes 1.85 and 0.00 per cent). Family II gave four such ears with a total of 333:30 (8.26 per cent; extremes 12.12 and 5.52 per cent). Family III gave one such ear with 58:0. Family IV gave nine such ears with a total of 1840:23 (1.23 per cent; extremes 2.22 and 0.00 per cent, one case). Family V gave three such ears with 638:51, or 7.40 per cent mottling; but that is not all. One of these ears gave 263:10. The other two were identical with respect to both their parents, both growing on the same plant. One of them gave 237:41, the other 138:0.

One hesitates to draw any general conclusion from these data. Certainly R tester does not contain that essential factor for mottling which was present in C tester. In the event that EMERSON'S C tester and R tester were extracted fairly recently from the same parent stock, the present situation might suggest that this unknown mottling factor was an attribute of EMERSON'S R factor itself, or at least closely linked. This, however, would involve some awkward, although not impossible, assumptions to explain the behavior of mottling in those families produced by crosses of C tester with EAST'S material; for, of course, the latter did not contain the mottling factor. The situation would be somewhat simplified if it were sweepingly assumed that the mottling which appeared in these R tester families (just described) was not true mottling at all, but just an imitation. True enough, mottling is at times fairly well imitated, but these particular imitations were so like the genuine

article that the writer is very reluctant to discard them. A safe tentative conclusion would be the following. The prime requisite for mottling is that the R factor enter with the male parent only; this perhaps is equivalent to saying "that the R factor be present in the endosperm in just one out of three possible doses." Under these circumstances mottling regularly occurs when there is also present that condition which is possessed and transmitted by most C tester individuals. A different condition, occurring in R tester, favors mottling in a small percentage of the possible cases, while the conditions present in EAST'S material permit of no mottling under any circumstances. The critical data should, of course, appear in the next generation.

Partial variability

The term "partial variability" has been used to indicate the variation which may occur between different parts of a single plant as regards any given character, without implying anything about the mechanism which may explain this variation. It is therefore preferable to "somatic segregation" for the present purpose. Preliminary tests of the possibility of partial variability in corn were conducted in two very simple and obvious ways. The first, so far as it went, gave such decisive and orthodox results that it may be summarized very briefly. With respect, at least, to the P, R, and C factors, pollen from suckers that had been allowed to develop was identical in crosses with that obtained from the main plant. Ears developed on such suckers were, if present, so poorly developed as to yield no adequate ratios; but ears produced on suckers that had been allowed to develop abnormally, through early removal of the main stem itself, gave the predicted ratios in all cases. These results discouraged carrying out any large scale test of this matter, at least as regards aleurone color. On the other hand, a few sporadic cases suggest that such manipulation might yield surprising results when applied to the inheritance of plant color, and particularly chlorophyll. The other method was to apply the same pollen to the silks of two of the ears on the same individual, and to compare the ratios obtained. Such attempts were frequently unsuccessful, owing to the inability of the plants

to develop two sufficiently well filled ears under the handicap of artificial pollination. Hence it was very common to get one full ear, while the other contained so few grains as to be practically worthless. This depends in part, of course, on the variety of corn used.

The bulk of the data obtained was on starchy-sweet and yellow-colorless ratios, and will be merely summarized at present: (1) the ratios were virtually identical on both ears, and (2) any marked deficiency of a given class on one ear always appeared in a strikingly

TABLE II

Ear	Count	Observed ratio	Predicted ratio
660	206:161	56.13:43.87	56.25:43.25
661	203:158	56.23:43.77	56.25:43.25
704	242:81	74.61:25.39	75.00:25.00
707	275:91	74.93:25.07	75.00:25.00
683	118:45	72.39:27.61	75.00:25.00
684	47:19	71.21:28.79	75.00:25.00
682	163:54	75.57:24.43	75.00:25.00
680	33:14	70.21:19.88	75.00:25.00
572	108:33	76.59:73.41	75.00:25.00
571	62:15	79.48:20.58	75.00:25.00
670	138:80	63.30:36.70	75.00:25.00
678	276:94	74.59:25.41	75.00:25.00
557	43:42	50.58:49.42	50.00:50.00
558	25:25	50.00:50.00	50.00:50.00

similar degree on the other ear. Relative to some of the ratios discussed earlier in this paper, representative data follow.

I. Colored-colorless ratios are markedly consistent for both ears, as may be seen from table II. The only decided inconsistency is between 670 and 678. There is little doubt that this inconsistency is real and significant, although it cannot at present be interpreted. One feels, however, like regarding this as an isolated exception.

II. Purple-red ratios are also about as consistent as could be expected (table III). Probably the only significant case is 682–680. Although the converse has been well demonstrated for other

ratios, it is altogether probable that such apparent deficiencies of red in a purple-red ratio, instead of being due merely to chance, are not only characteristic of given individuals, but heritable to some

TABLE III

Ear	Count	Observed ratio	Predicted ratio
660	155:51	75.24:26.76	75.00:25.00
661	152:51	74.39:25.61	75.00:25.00
704	182:60	75.20:24.80	75.00:25.00
707	204:68	75.00:25.00	75.00:25.00
683	89:29	75.42:24.25	75.00:25.00
684	38:8	80.85:19.15	75.00:25.00
682	132:31	80.98:19.02	75.00:25.00
680	29:4	87.87:12.13	75.00:25.00
670	101:37	73.19:26.81	75.00:25.00
678	212:64	76.81:23.19	75.00:25.00
571	52:10	80.64:19.36	75.00:25.00
572	76:32	70.37:29.63	75.00:25.00

TABLE IV

Ear	Count	Observed ratio
660	202:4	98.06:1.94
661	202:1	99.51:0.49
704	242:3	98.77:1.23
707	272:6	97.84:2.16
683	106:12	89.83:10.67
684	42:5	89.37:10.63
682	154:9	94.48:5.52
680	29:4	87.87:12.13
571	58:4	91.91:8.09
572	84:24	77.77:22.23
670	130:0	100.00:0.00
678	235:41	85.14:14.86

degree. It must be realized, however, that such deficiencies of red are probably apparent rather than real; improper classification may throw dark red grains with purple, but it may well be that the border line is thus obscured through some heritable tendency.

III. If one is to regard true mottling as limited to those cases in which the character appears in *all* the grains which receive R from the male parent only, that is, descendants of C tester, then, unfortunately, no data are at hand on comparative mottling ratios in two ears with the same parents. Such data, however, are available from descendants of R tester, where mottling (or pseudo mottling, as it may prove to be) appeared in relatively small percentages, as shown in table IV. The discrepancies apparent in table IV may be taken to indicate that the supposed mottling of the R tester line is altogether sporadic and without genetic significance. Even though that may be so, the surprising case of 670–678 is probably worthy of further investigation.

IV. Among the progeny of the faint colored grains only two poor examples of this sort are available, as may be seen in table V.

TABLE V

Ear	Count	Observed ratio
	Faint : Colorless	
562.....	17:46	26.98:73.02
563.....	26:104	20.00:80.00
557.....	0:42	0.00:100.00
558.....	9:16	36.00:64.00

It is highly probable that the occurrence of these faint grains is sufficiently limited by local conditions so that discrepancies between two such ears will prove common. This is also suggested by the results of a test which need only be briefly mentioned at present.

It is expected that the numerical value of any ratio, which is affected only by matters Mendelian, will conform with predictions based on the laws of chance. With equal certainty the laws of chance indicate that, where a 1 colored : 1 colorless ratio appears, we will not find many long strings of colored grains lying together in the same row. Actually we may expect that the colored grains will be scattered within the rows of the ear in such a way that there will be, speaking relatively, n groups of 1 colored grain each, n/2 groups of 2, n/4 groups of 3, etc. These values will differ, of course, with the ratios themselves. Thus, in a 3 colored : 1 colorless,

there will be n groups of 1 colorless, n/4 groups of 2, n/16 groups of 3, etc.; while, for the colored grains, there will be n groups of 1, $\frac{3n}{4}$ groups of 2, $\frac{9n}{16}$ groups of 3, etc. The exact values can easily be calculated for any ratio, although they frequently must be carried to several decimals. Such a test was applied to numerous types of ratios, and also, for purposes of control, to the tossing of coins (singly or in groups, depending on the ratio). The purpose of the test was to discover whether any of the characters under consideration were determined or limited by local conditions within the ear. Preliminary tests of this sort showed that starchy-sweet and colored-colorless ratios depended only on laws of chance. When the test was applied to the self-colored-mottled ratios of the C tester progeny, the laws of chance were fairly well satisfied, but, undoubtedly, to a less degree than in the other cases. Such slight nonconformity as occurred, however, might well have been accounted for by difficulties in classification. Tests applied to the mottling of the R tester progeny were not thought to be significant, owing to the very small percentages of the mottled grains appearing. With the particolored grains, however, very decisive results were obtained, indicating clearly that local conditions on the cob affect the appearance of this character. Thus in ears on which less than 10 per cent of the grains were particolored, the majority of the total number of such grains was made up of a few groups of 4 or 5 each. This is particularly interesting, since it has been demonstrated that this condition is heritable. The puzzle will probably be solved by finding that local conditions on the ear do not determine, but merely limit, the appearance of the particolored condition. It is expected that some, but not all, of the seemingly quite colorless grains from these ears will perpetuate the particolored tendency.

Summary

1. The use of the corn-pollinator is recommended to amateur investigators.

2. The P(Pr), R, and C factors for aleurone color, variously combined, gave predictable and readily distinguished ratios.

3. In many cases the exact genotype, with reference to the R and C factors, can be distinguished by superficial appearance.

4. The particolored grains of EAST and HAYES were identified. In these some partial substitute enables the P and R factors to express themselves, even in the absence of C. This substitute is heritable, but its effectiveness is limited by local conditions in different parts of the ear or of the plant as a whole.

5. Mottling (EMERSON), which occurs when the R factor comes in with the male parent only, is conditioned by the presence of a heritable factor or factors. This factor occurs in the C tester family, and is dominant in crosses with families which do not show mottling. The R tester family seems to contain a different factor, which produces apparent mottling only in a small percentage of the expectations.

UNIVERSITY OF CHICAGO